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Effect of social defeat in a territorial bird (*Parus major*) selected for different coping styles

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Abstract

We addressed the questions (i) whether a social defeat triggers similar autonomic and behavioral responses in birds as is known from mammals and (ii) whether individuals that differ in coping style differ in their reaction to a social defeat. Adult captive male great tits (*Parus major*) from either of two different selection lines for coping style were used to test the effect of social defeat by an aggressive resident male conspecific on subsequent social and nonsocial behaviour, body temperature, breath rate and body mass. These parameters were measured 1 day before (baseline), immediately after and at Days 1 to 3 and 6 after the social interaction took place (Day 0). Social defeat decreased social exploration and increased body temperature substantially for at least 1 day in all birds. Breath rate and body mass were not affected. Birds belonging to the more aggressive and bolder line showed impairment in activity immediately after the social defeat. This is to our knowledge the first report showing that psychosocial stress in birds can have a similar impact as in rodents, but with a shorter recovery time. This might be due to species-specific differences in sensitivity to social stress, or to differences in the way social stress was induced.

Keywords: Social defeat; Stress; Great tit; Body temperature; Breath rate; Activity; Coping

1. Introduction

In many species animals are frequently faced with different levels of stress deriving from interaction with conspecifics. Proximate mechanisms and dynamics of an organism's reaction to psychosocial stress have been broadly investigated in animals especially in the framework of stress-related pathological diseases [8,10,23]. Yet, most of the work is restricted to mammals, in particular rodents and primates, exposed to severe or chronic stress procedures (e.g., prolonged social isolation, housing in overcrowded environments or early maternal separation) very unlikely to occur in the real world. An attempt to modify this approach has been made by testing the effect of social defeat in territorial animals, mainly rodents [11,14,15,17,19]. These studies clearly showed that this paradigm provides a powerful and realistic methodology to study strategies to cope with naturalistic stress [9]. In rodents a social defeat affects the organism both at the physiological and behavioral level [9,11], with a general increase in sympathetic activity (heart rate and body temperature) lasting from one to several hours [12] and an impairment of social and explorative activity lasting up to several weeks [14]. Effects of social defeat have never been tested in birds although it is known that nestlings' activity and heart rate are very sensitive to an alarm call [18], which in many species is often emitted during fights.

Individuals may greatly differ in the way they respond to stress. Over the past decade, it has become clear that such differences may reflect basic differences in the way individuals deal with challenges. These differences can be expressed in many physiological and behavioral domains, have a strong genetic basis, and are the reflection of so called coping styles [10]. Similar types of coping styles have been established for several domesticated species. Recently, evidence has accumulated that two coping styles exist in the

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great tit (*Parus major*), a wild bird species [13,20,21]. Great tits are classified as fast or slow on the basis of the scores obtained in two exploration tests (each calculated in classes of 0 to 10) carried out at the age of 30–40 days after hatching: In the first test the latency to approach a novel object placed in the individual's home cage is measured; in the second test, the time taken to visit five artificial trees in an unfamiliar environment is measured. Consistent individual differences in these tests were observed along an axis ranging from slow but thorough explorers to fast and superficial explorers [20]. Artificial selection combined with cross fostering resulted in clear evidence for the genetic basis of these traits. The offspring scores correlated with those of the mean of the parents and rapidly diverged between the two lines after two generations. Further characterization has shown that the fast explorers are also aggressive, prone to form routine and tend to copy the foraging habits of a conspecific tutor, while the slow explorers rarely start a fight, do not follow a routine and tend to use less the information in foraging coming from a tutor [13,20,21]. Overall the two styles share striking similarities with the SAL (short attack latency) and LAL (long attack latency) mice, an important model for coping styles [1,10,16].

In a study on social dominance in aviary flocks of both lines it was reported that fast individuals, being more aggressive than slow birds, were usually either dominant or totally subordinate. The latter might be explained by the fact that the fast birds took more time to recover from a defeat than slow individuals, as measured from the higher latencies to initiate a new interaction [22]. This suggests that social defeat in these birds may have a large impact on subsequent behaviour and is dependent on the coping style of the individual.

With this study we wanted to verify (i) whether the social defeat paradigm known to cause signs of stress in mammals triggers similar autonomic and behavioral responses in birds and (ii) whether individuals of the fast and the slow type of great tits also differ in the way they cope with a social defeat.

The great tit is a passerine, territorial, nonmigratory bird (body mass 16–20 g) inhabiting woods and parks. Males start establishing their territory already in winter, thereafter forming monogamous pair bonds. Intermale competition and social conflicts are very common, including a well-defined repertoire of agonistic behaviour [2,24] displayed both in territorial contests and in foraging flocks. We tried to design the experiment in such a way that the social defeat occurred in an ethologically meaningful way, like in the real world where birds often try to invade another territory and are defeated and chased away by the territorial owner.

Before and after the defeat we measured a number of physiological and behavioral parameters known to be affected by psychosocial stress in rodents (body temperature, social behavior, activity) and by handling stress in birds [4]. It was not possible to measure cardiovascular parameters, but breath rate was assumed to respond similarly to heart rate since both are part of the adrenergic stress response.

2. Materials and methods

2.1. Subjects and housing

The experimental birds were 16 adult male great tits originating from a program of bidirectional artificial selection started in 1993 on the basis of the outcome of exploration tests carried out at the age of 30–40 days [13,20]. The birds used belong to the F3 and F4 generation, 6 of the slow, and 10 of the fast line. In addition, 7 unselected males were used as stimulus birds (see below). Birds were individually housed in standard cages ($80 \times 40 \times 40$ cm) with wooden bottom, top, side and rear walls, a wire-mesh front and three perches. The bottom was covered with shellsand. A small empty cage to be used for the social exploration test (see below) was hanging on a side of the cage. The birds were kept on a light–dark cycle of 8:16 h and were provided with ad libitum water, sunflower seeds and a commercial dry mixture (proteins, trace elements, minerals and vitamins). Every 2 days the animals were provided also with a fresh mixture of raw heart, insects, proteins, trace elements, minerals and vitamins. Live mealworms (*Spodoptera exigua*) were given three times a week.

For the social defeat and the tests (see below) an experimental bird was transferred to a cage, similar as the home cage, 3 days before the social defeat was given and remained there until Day 6 after the social interaction (Table 1).

2.2. Social defeat

Adjacent to the cage of the experimental bird an identical cage was positioned, containing one of two so-called resident birds. Experimental birds were randomly allocated to these two resident males. The latter were kept in these cages under the same housing conditions of the experimen-

Table 1
Time course of the tests

Day −4	BM and transfer to the experimental room
Days −3 to −1	Habituation
Day −1	BT, BR, H, SE, training
Day 0	**SI1, H, SI2, SE**
Day 1	BT, BR, H, SE
Day 2	H, SE
Day 3	BT, BR, H, SE
Day 6	BT, BR, BM

In bold, the day in which the defeat occurred. See Materials and methods section for details of the procedures. BM = body mass; BT = body temperature; BR = breath rate; H = hopping test; SE = social exploration test; SI = social interaction.

tal birds for several weeks to become territorial. The two resident birds were adult males of unknown genetic background and unknown coping style chosen on the fact that they always attacked an intruder male in a series of 5-min tests. The cages of the experimental and the resident birds were separated from each other by a removable opaque partition. The cage of the resident contained an identical removable partition that divided the cage in two equal parts. During the day before the social interaction (Table 1) the experimental birds underwent a series of five training sessions to allow the social interaction to occur without stressful procedures such as handling or forced chasing. Each session consisted in confining the resident bird to one half of his cage and placing a dish with mealworms in the remaining part of the cage. The partition dividing the resident's cage from the cage of the experimental bird was opened allowing it to enter and eat one mealworm. During the next day the social interaction took place in the cage of the resident between 0930 and 1030 h according to the following procedure: (1) the resident bird was confined with the same procedure used for the training sessions; (2) after few seconds the partition dividing the cage of the resident from the cage of the experimental bird was removed; (3) as soon as the experimental bird entered the area (due to the training this occurred within 10–30 s), the partition separating the cages was closed, the partition confining the resident male was removed and the social interaction started. After the social interaction, the original situation was reinstated. The removal of the partitions was remotely controlled by means of ropes. The resident bird was always exposed to a maximum of two interactions per day and before the social interaction it was not provided with new food as it usually happened in the morning. In order to reduce the possible effect of time elapsing between the social interaction and the social exploration test, due to the measurements of hopping (which lasted 5 min, see below and Table 1), a second interaction with a standard cut-off time of 5 min was given to the experimental bird immediately after the hopping measurement with the same resident male and the same procedure described above.

The first interaction was stopped after 20 min or as it escalated, i.e., when one of the following three criteria was met: (1) one of the two birds was sitting quietly (freezing) for 5 min, (2) being chased for 3 min, or (3) being attacked for 10 times. When one of the criteria was met by the experimental bird, it was considered defeated, when one of the criteria was met by the resident, it was considered the winner. In those cases in which an experimental bird did not meet any of the criteria, its behavior during the interaction was compared with that of clearly defeated birds and winners of a larger sample size ($N=10$ defeated and 7 winners) that included tests of a pilot study. In these tests clearly defeated birds showed lower values of percent interactions initiated ($t=-3.7$, $df=15$, $P=.002$), higher values of percent escape following approach by the resident ($t=2.24$, $df=15$, $P=.04$), and a higher frequency of crest raising ($t=3.33$, $df=15$, $P=.005$) respect to winners. We concluded that during an interaction these parameters are indicators of defeat. Therefore we considered a bird defeated when its values of at least two of the three parameters fell within the ($\pm$) standard error of the mean value of the clearly defeated animals. The designation of each bird agreed with the subjective impression of two independent observers that were familiar with the behaviour of great tits. Following the three criteria and the behavioural evaluation, 6 of 6 slow birds and 6 of 10 fast birds (Fisher's exact test, $P=.11$) were considered defeated.

2.3. Tests

2.3.1. Body temperature, breath rate and body mass

Body temperature was measured with a thin flexible probe kept in warm water and inserted via the beak in the throat for 3 cm. Data were collected during the end of the dark period (early morning) because in darkness catching time is extremely short (1–10 s) minimizing possible confounds from catching stress. Immediately after the temperature measurement, breath rate was measured during 4×15 s by keeping the subject in the hand. Values were significantly lower in the last 15-s block, $F(1, 15)=8.57$, $P=.01$, and these were used for further analyses as they were thought to be closest to the basal levels. Birds were weighed twice, before the start of the experiment and at Day 6, with an electronic balance to the nearest 0.01 g.

2.3.2. Social exploration

Each home cage contained a small wire cage attached at the outside of the wire front. An identical one with an unfamiliar male inside replaced this cage. Five 2-year-old males of unknown coping style raised in captivity under similar condition as the experimental birds were used as stimuli. They were housed in the experimental room 1 week before the start of the experiment. Time spent on the perch closest to the stimulus during 5 min after the first approach was measured with a Psion event recorder and processed with the software Observer 3.0. As this social challenge was given on five successive days to each bird, five different birds were used, each for every test. The sequence of the birds differed between the experimental subjects. The first observation following social defeat was performed immediately after the second social interaction in order to look at short-term consequences.

2.3.3. Hopping

Frequency of movements from perch to perch in the home cage was counted during 5 min as a measure of normal activity. The first observation took place immediately after the end of the first social interaction in order to look at short-term consequences. Subsequent observations were taken immediately before the social exploration test.

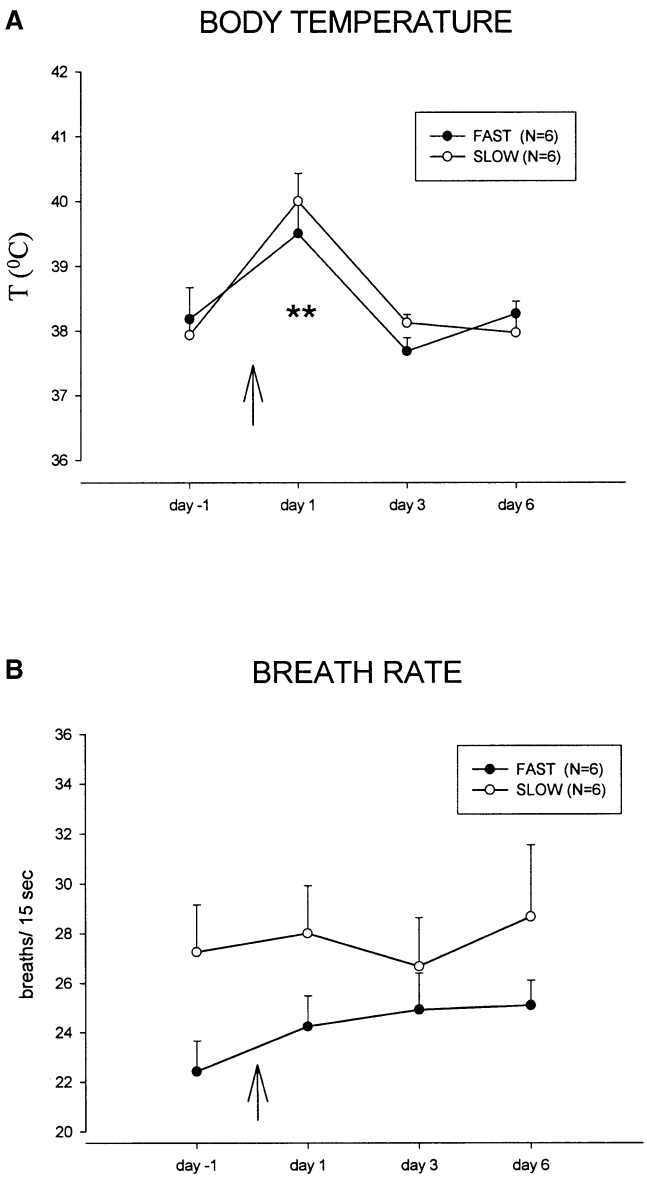

Fig. 1. Time course of mean (+S.E.M.) body temperature (A) and breath rate (B) before and after the social defeat (indicated by an arrow). In graph A ** indicates significant difference ($P<.01$) in birds of both lines between Days 1 and −1.

The time course of the experiment and the sequence of tests are shown in Table 1. The birds were tested in series of four birds, the sequence of tests lasting 10 days/series. The tests were carried out in January and February 2000. The birds were assigned to the series randomly, but care was taken to alternate fast and slow individuals within the series. Observations of the birds in the experimental room were done through holes (20 cm in diameter) in the wall of the room.

2.4. Statistics

Data were analyzed with SPSS 9.0. Baseline levels were tested for normality with a Kolmogorov–Smirnov test and a normal probability plot. In case of nonnormality data were arcsine transformed in case of percentages and ln transformed in the other cases. Student *t* tests for independent samples were used to test for effects of type (fast or slow) on baseline levels. An analysis of variance for repeated measurements was used to test whether scores obtained during the different days

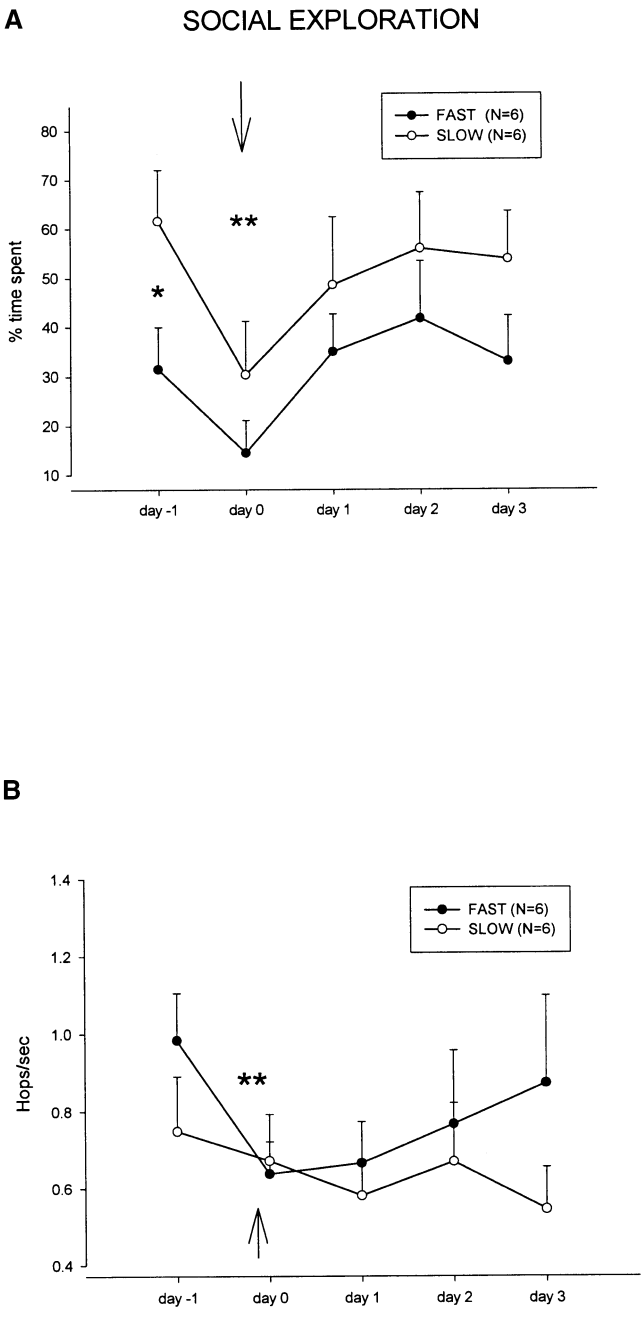

Fig. 2. Time spent on the perch close to the stimulus male (A), and hopping rate (B) before and after the social defeat (indicated by an arrow). Data are means+S.E.M. In graph A ** indicates significant difference ($P<.01$) in birds of both lines between Days 1 and −1 and * indicates significant difference ($P<.05$) in baseline levels; in B ** indicates significant difference ($P<.01$) in birds of the fast line between Days 0 and −1 and Days 1 and −1.

after the social defeat differed from the basal levels before social defeat (within-subject factor), and whether birds of the different selection lines differed in their responses (between-subjects factor, and the interaction effect between both factors). In this test, we used a simple contrast by which the data of each day are compared with the basal levels.

3. Results

3.1. Basal line differences

Social exploration was significantly, ($t = 2.23$, $P = .05$) and breath rate almost significantly ($t = 2.11$, $P = .06$) higher in slow than in fast birds (Figs. 1b and 2a), while the lines did not differ in the other two parameters.

3.2. Effects of social defeat

Body temperature showed a clear rise in both lines at the first morning after the social defeat (Fig. 1A), $F(1,10) = 14.7$, $P = .003$. Thereafter the values were returned to baseline levels ($P = .55$). Breath rate (Fig. 1b), and body mass were not affected ($P = .27$). Time spent close to the stimulus bird in the social exploration test was markedly decreased in both lines during the day of the defeat, $F(1,10) = 10.9$, $P = .008$. The scores returned to baseline levels already the first day after the challenge (Fig. 2a, $P = .45$). Hopping activity was reduced immediately after the challenge (Fig. 2b), $F(1,10) = 6.8$, $P = .026$. During Days 1 and 2 the scores were still suppressed, $F(1,10)$, 30.0 and 4.0, respectively, $P = 0.01$ and 0.07, respectively. At Day 3 the values were almost back to basal levels, $F(1,10) = 0.92$, $P = .36$.

3.3. Line differences in reaction to defeat

In none of the comparisons of the postdefeat measurements with predefeat measurements was a significant interaction effect found between line and day. This indicates that we could not show line differences in the reaction to the social defeat. However, in the hopping scores the decrease after defeat was mainly due to the fast line, Day 0 vs. Day -1, $F(1,5) = 17.1$, $P = .009$, while the change over time in the slow line was not significant, Day 0 vs. Day -1, $F(1,5) = 1.26$, $P = .23$.

4. Discussion

In the present study a social defeat in a territorial bird has been shown to: (i) increase substantially body temperature for at least 1 day; (ii) have no clear effect on breath rate and body mass; (iii) impair activity (hopping) for at least 2 days; and (iv) decrease substantially approach to an unknown conspecific in the very short term.

These results are to our knowledge the first to show the impact of a social defeat in a bird species. These are in several aspects similar to the effects of social defeat described in rodents. The increase in body temperature shows resemblance to the phenomenon of emotional fever, found in other animal species. This resemblance is further strengthened by the finding that emotional fever, but not hyperthermia, reaches a higher level at night than during daytime [3], and our data were collected at the end of the dark phase. Furthermore, emotional fever has been shown to occur in birds, as well as in reptiles, in response to gentle handling and manual restraint [4,5]. However, further studies of the physiological control of the rise in body temperature in the great tit are needed to distinguish between a genuine fever, characterized by an upward shift of the set-point temperature, and hyperthermia, characterized by a rise in central temperature above the set-point temperature due to an increase in heat load [3]. In other species, a social defeat has an effect lasting at least 4 days [12] whereas here after 2 days baseline values were completely recovered. In addition, in pigs normal values after mixing are recovered within 8 h [6]. In our case, the rise in temperature was observed 18–20 h after the social defeat. Although the measurement of body temperature seems to be a severe stress per se, it is unlikely that the observed change was due to the handling procedure because it occurred only in the day after the social defeat.

The absence of clear effects on breath rate might be due to the fact that this parameter reflects the activity of the adrenergic system, whereas an increased activity of this system is usually observed only in the very short term after exposure to a stressor (from minutes to hours).

General activity, measured by counting the frequency of hopping from perch to perch, was suppressed for a substantial period after the social defeat. This is similar to what has been found in rodent studies [11,14]. A clear suppressive, but shorter lasting, effect was also found in social exploration. After the social defeat birds tended to avoid an interaction with a conspecific, even in the case that this conspecific was a different bird than the one they had experienced during the previous social defeat. Latency to approach the conspecific, probably the best parameter to test the prediction that fast animals take more time to initiate a new social interaction after a defeat than slow animals [22], could not be measured reliably in our small housing cages. Some support for this prediction comes from the observation that in the fast line activity was more markedly reduced than in the fast line during the hopping test. This might relate to longer latencies to start a new interaction as measured in a large aviary [22].

Although the results are quite similar to those obtained with rodents, the time span of the effects in our birds is relatively short. This might be due to either species-specific differences in the sensitivity to the stressor, or to a difference in the experimental design. Rodents or primates often live in groups with a stable social structure where serious agonistic

interactions are uncommon. The great tit is a territorial species, and short-lasting fights are very common, both during territorial establishment when competitors arrive simultaneously in a vacant area and in the establishment of dominance hierarchies in nonterritorial winter flocks [7]. Moreover, in case of a defeat great tits can easily avoid the opponent or change flock. In rodents and primates animals are much more dependent on the group in which they live. The difference in the experimental design is an obvious possibility too. In those rodent studies in which an acute stress procedure is employed (single social defeat), the confrontation between the resident and the intruder is often much longer in duration, and includes more fights, while in our case the confrontations were ended as soon as the interaction escalated. Furthermore, in rodent studies the loser is exposed to the winner after the social defeat for a substantial period. Since this would be a highly unnatural situation for a bird like the great tit, our second exposure lasted only 5 min.

Nevertheless, we did find a clear impact of a social defeat in our species within our design. This strongly suggests that in the natural situation a social defeat has important consequences for the loser. We view these effects as falling within the range of the classical adaptive stress response rather than being pathological [12]. The rise in body temperature might be beneficial to deal with pathogens that have an increased chance to infect the body after a fight, due to wounds obtained during that fight. A lower activity and a reduced tendency to approach conspecifics might be the consequences of an emotional fever (sickness behavior), serving the function to reduce the chance of a social interaction while being in an impaired condition.

Based on previous findings it was hypothesized that birds from the fast selection line would suffer more strongly from social defeat than birds from the slow line [22]. However, we found only some evidence for this in the suppression of general activity. Since the birds have been selected based on their juvenile behavior, there is the possibility that certain phenotypic differences in behavior are not present at the adult stage. This is, however, unlikely. Basal levels of social exploration were significantly higher in the slow birds relative to the fast birds. This fits the expectation, since slow birds are selected for high levels of exploration and fast birds for low levels of exploration in an unfamiliar environment and in novel object tests [20]. Furthermore, the line difference in breath rate before the defeat was borderline significant. Other differences between the lines in adulthood have been found in agonistic behavior and latency to approach a novel object (Carere and Groothuis, unpublished results) in adult birds of the same generation of selection line.

We conclude that in birds psychosocial stress due to a social defeat can have a similar impact on behavior and physiology as in mammals, but with a shorter recovery time, therefore falling within the range of the classical adaptive stress response. According to the expectation, individuals more aggressive and bolder in exploration (fast line) seem to suffer a stronger impact from a social defeat, but only in activity levels. The next step in this field of research that has to be taken is the analysis of the consequences of social defeat in different types of individuals in the natural situation. This would allow us to translate the finding from the individual to the population level via the analysis of the consequences of stress sensitivity for survival and reproduction.

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